

# A New Superfamily in the Extensive Radiation of South American Paleogene Marsupials

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## ABSTRACTS

Significant new mammals have been recovered from the Colhuehuapian mammal-bearing beds (latest Oligocene) exposed in the Gaiman region of Patagonia (Chubut Province, Argentina). Some fragmentary mandibles and isolated teeth belong to a new genus and species, **Patagonia peregrina**. The mandibular and dental specializations of this form are so distinctly convergent on those of some fossorial rodents that it is regarded as a distinct clade of South American marsupials. It represents the type of a new family, **Patagoniidae**, which is assigned to a new superfamily, **Patagonioidea**, which represents a natural evolutionary group in the same sense as other superfamilies of marsupials recognized by Simpson. Its systematic position within the superorder Marsupialia awaits comprehensive analysis of those enigmatic marsupials (Groeberioidea and Argyrolagoidea) apparently most closely related to it.

Varios nuevos y significativos mamíferos han sido recogidos de capas mamalíferas del Colhuehuapense (Oligoceno tardío) expuestas en la región de Gaiman, Patagonia (Chubut, Argentina). Algunos fragmentos mandibulares y dientes aislados pertenecen a un nuevo género y especie, **Patagonia peregrina**. Esta forma presenta especializaciones mandibulares y dentarias tan distintamente convergentes hacia las de algunos roedores cavadores que es considerada como un distinto clado de marsupiales sudamericanos. Representa el tipo de una nueva Familia, **Patagoniidae**, que es asignada a la nueva Superfamilia **Patagonioidea**, porque representa un grupo evolutivo natural como los de otras Superfamilias de marsupiales reconocidas por Simpson. Su posición sistemática dentro del Superorden Marsupialia depende del análisis integrado de aquellos marsupiales enigmáticos (Groeberioidea y Argyrolagoidea) aparentemente más estrechamente relacionados a él.

Novos mamíferos foram recuperados dos leitos de Colhuehuapian (do alto Oligoceno), expostos na região de Gaiman, Patagonia (Província de Chubut, Argentina). Fragmentos mandibulares e dentes isolados pertencem a um novo genero e espécie, **Patagonia peregrina**. As especializações mandibulares e dentais encontradas são tão claramente convergentes às de alguns roedores fossórios, que esta forma é considerada uma classe distinta de marsupiais sulamericanos. A espécie representa o tipo de uma nova família, **Patagoniidae**, a qual é designada a uma nova superfamília, **Patagonioidea**, por formar um grupo evolutivo bem definido, como o formam as outras famílias de marsupiais, reconhecidas por Simpson. A posição sistemática dos Patagonioidea, dentro da superordem Marsupialia, aguarda uma análise mais compreensiva dos marsupiais ainda enigmáticos (como Groeberioidea e Argyrolagoidea) aparentemente e seus relativos mais próximos.

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## Introduction

The taxon described in this paper is yet another example of the great adaptive radiation and dispersal of marsupials in South America. It represents a second line of marsupials that is convergent on the rodent adaptive zone (cf. Groeberioidea—Patterson, 1952; Simpson, 1970c; Clemens & Marshall, 1976). However, it is distinct from previously named forms, not only phylogenetically but also ecologically.

The new form does not suggest that marsupials attained the breadth and diversity of rodent adaptations, but it does show that marsupials occupied the rodent adaptive zone in previously unimagined ways. This new marsupial indicates that marsupial radiations in South America were almost as broad and reached as great extremes as those in Australia. The find is consistent with the view that "A complete record of South American marsupials would certainly include a large number of taxa, probably some of high categorical rank, now unknown" (Simpson, 1970a, p. 59). This and other forms recently found in northwestern Argentina (Pascual, 1980a, b, 1981, 1983) validate Simpson's prophetic suggestion that "... major parts of marsupial evolution were occurring in areas and facies inadequately sampled, if at all, by the known fossil deposits and the collections so far made" (Simpson, 1970a, p. 58). These deposits indicate the value of applying new sample-collecting techniques at mammal-bearing localities that are supposedly well known; it is only necessary to find new, appropriate facies.

The new ecological type from the Paleogene provides evidence to support Gould's (1983) view of "early experimentation, later standardization," with a consequent reduction in diversity. As in therians (Pascual et al., 1985) the diversification of South American marsupials took place principally in the Paleogene.

Measurements reported in Table 1 are depicted in Figure 3 and are given in millimeters. The abbreviation MACN CH is used for the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires), Colección Chubut.

## Classification

### Superfamily PATAGONIOIDEA nov.

The only known family of this taxon is the Patagoniidae. The superfamily is sufficiently charac-

terized by the diagnoses of that family and its only known species. Justification for its superfamilial rank is given in a later section on affinities.

### Family Patagoniidae nov.

TYPE—*Patagonia* gen. nov. The only known genus.

KNOWN DISTRIBUTION—Late Oligocene. Colhuehuapian from Central Patagonia (Chubut Province, Argentina).

DIAGNOSIS.—Small marsupials with the same reduced number of lower teeth as the Groeberiidae, but with a different dental formula: 1.1.0.3. Open-rooted and rodent-like lower incisor, oval in cross section, strongly curved, although not as much as in the Groeberiidae, and with the intra-alveolar portion differently arranged. The incisor extends lingually along the ventral border of the mandible to the root of the inflected crest beneath the last molar, where it forms a prominence similar to that of hystricognathous rodents, but ventrally. Lower canine smaller, procumbent, apparently incisor-like and closed-rooted, separated from the cheekteeth by a short, crested diastema at alveolar level. Lower cheekteeth rectangular in cross section, decreasing in size posteriorly, hypselodont, rootless, wholly surrounded by enamel, and slightly curved, with the concavity forward. Horizontal ramus of the mandible short and deep, with the highest part posterior, beneath the masseteric fossa, where the body of the mandible becomes strongly convex and inflected; deep pterygoid fossa, limited ventrally by a flange like that found in Argyrolagidae and in some Australian marsupials (e.g., Macropodidae); strong, salient coronoid process; masseteric fossa relatively deep but reduced, dorsally situated with a prominent masseteric crest; subvertical symphysis unfused, with nearly smooth symphyseal surfaces.

### PATAGONIA gen. nov.

ETYMOLOGY—From Patagonia, its geographical record.

TYPE—*Patagonia peregrina* sp. nov.

KNOWN RANGE AND DIAGNOSIS—Same as that of the family.

### *Patagonia peregrina* sp. nov. Figures 1–3

ETYMOLOGY—From Latin *peregrinus*, strange or rare.

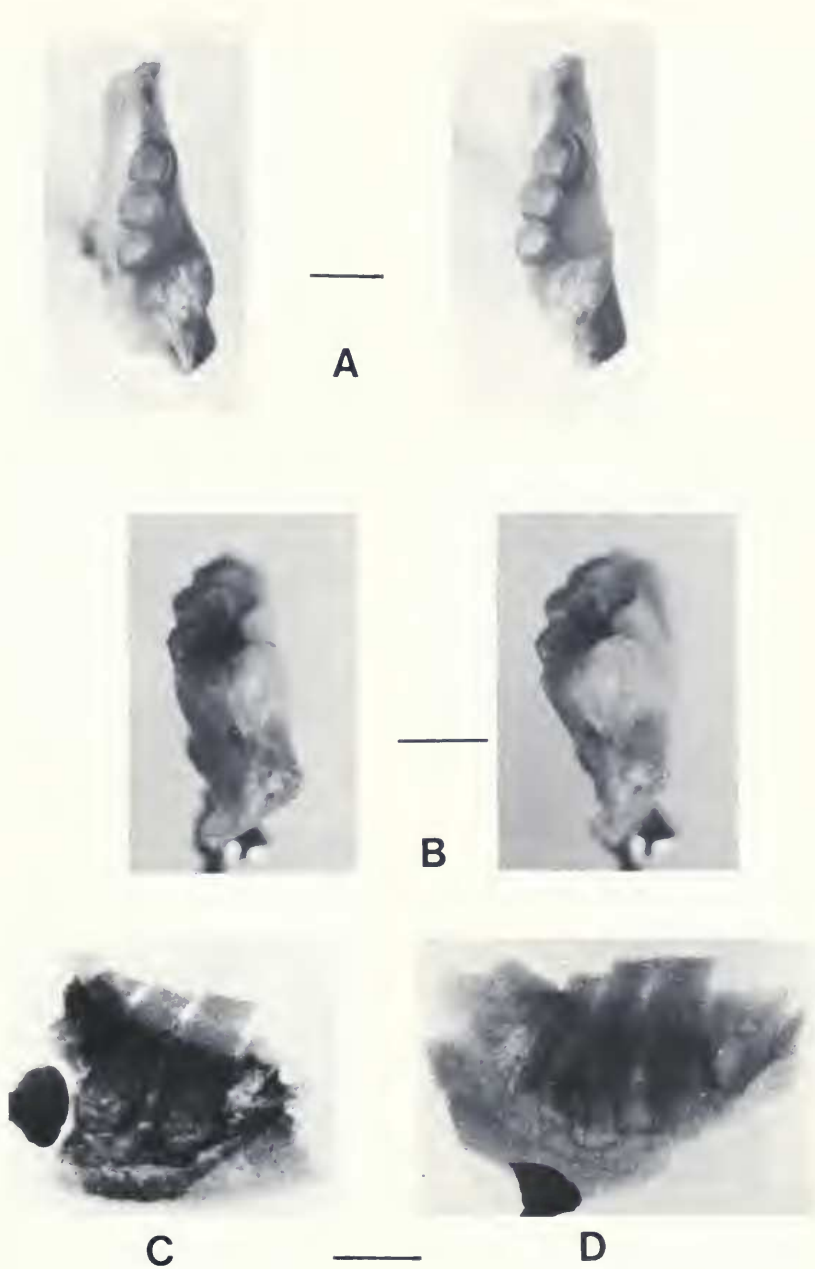


FIG. 1. *Patagonia peregrina* gen. et sp. nov. A-B, Stereopairs of MACN CH-865, a fragment of a right mandibular ramus with  $m_{1-3}$ : A, occlusal view; B, posterior view; C-D, X-ray of fragments of two right mandibular rami with  $i_1$ , alveolus of  $c_1$ , and  $m_{1-3}$  complete (C, holotype; MACN CH-869) and with alveoli of  $i_1$ , and  $c_1$ , and  $m_{1-3}$  complete (D, MACN CH-865). Graphic scale = 2 mm.

HOLOTYPE—MACN CH-869 (fig. 2A-B). Fragment of right mandibular ramus with three cheekteeth, intra-alveolar portion of the incisor, and alveolus of the canine.

HYPODIGM—Holotype and the following:

MACN CH-864, part of right mandibular ramus with first and second cheekteeth, part of alveolus of the third, and part of alveoli of incisor and canine; MACN CH-865, part of right ramus with three cheekteeth and alveoli of the incisor and

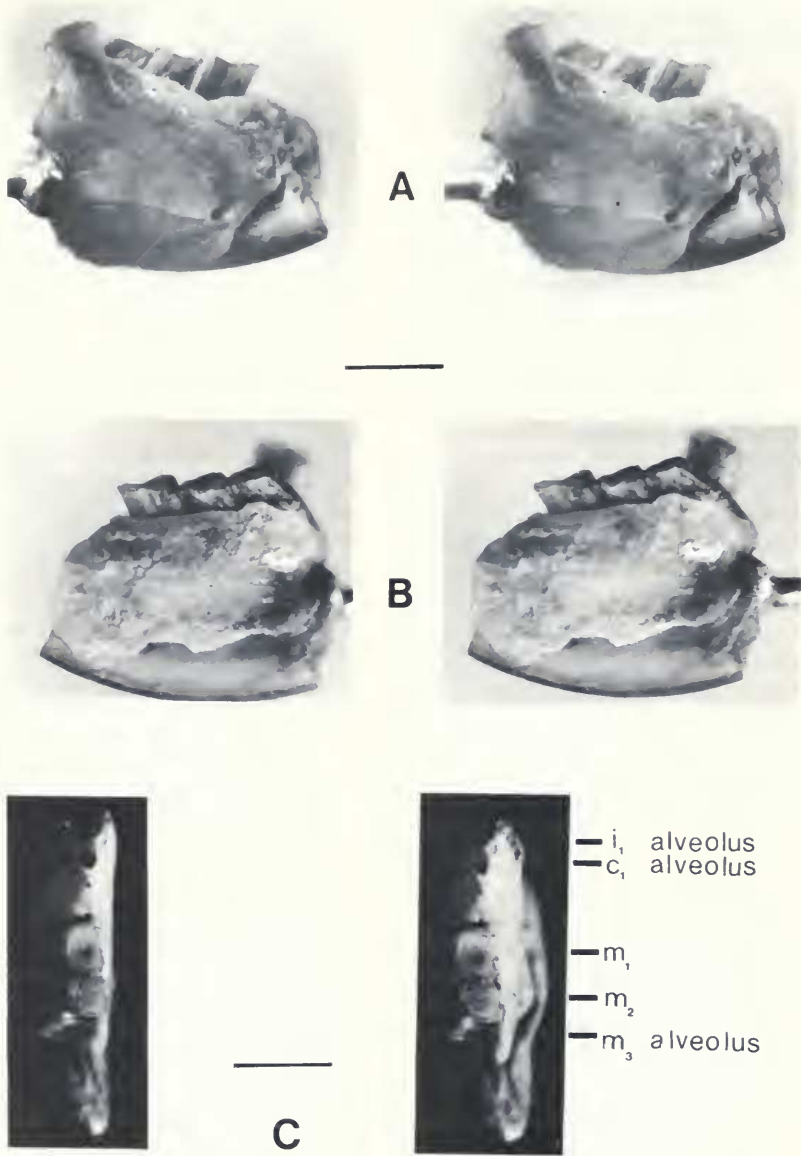


FIG. 2. *Patagonia peregrina* gen. et sp. nov. A-B, Stereopairs of MACN CH-869 (holotype), a fragment of a right mandibular ramus, with  $i_1$ , alveolus of  $c_1$ , and  $m_{1-3}$ ; A, labial view; B, lingual view. Graphic scale = 2 mm. C, Stereopairs of MACN CH-867, a fragment of a left mandibular ramus, with alveoli of  $i_1$ ,  $c_1$  and  $m_3$ , and  $m_{1-2}$ ; occlusal view.

canine; MACN CH-866, part of left ramus with the second and third cheekteeth, and part of alveoli of the first cheektooth and the incisor; MACN CH-867, part of the left ramus with the first and second cheekteeth, and part of alveoli of the third cheektooth, incisor, and canine; MACN CH-868, part of the right ramus with three cheekteeth and

alveolus of the incisor; MACN CH-870, part of left ramus with first and second cheekteeth and part of the alveolus of the third; MACN CH-874, part of right ramus with the second cheektooth, alveoli of the first and third cheekteeth, and part of the alveolus of the incisor; MACN CH-875, part of right ramus with the second and third

cheekteeth and part of the alveolus of the incisor; and MACN CH-876, three isolated upper(?) cheekteeth.

**HORIZON AND LOCALITY**—Both the holotype and the hypodigm come from the Trelew Member of the Sarmiento Formation (see Mendía & Bayarsky, 1981) and are Colhuehuapian (Late Oligocene) in age. Apparently they were found in the upper unit, exposed on the south side of the Chubut River valley, Chubut Province, Argentina (Central Patagonia; see Fleagle & Bown, 1983, pp. 242–244). Quite probably this corresponds to Simpson's "stratum *F* of Fig. 1," which is part of his "Trelew beds" (= "Trelewense"). The material was recovered by O. E. Donadío, M. Soria, J. G. Fleagle, and T. M. Bown (see Fleagle & Bown, 1983) through dry-screening local deflation lag deposits.

**DIAGNOSIS**—The only known species of the family.

**DESCRIPTION**—**Dentition**—See Figures 1A,C–D; 2–3. Each side of the lower jaw has one fully rodent-like gnawing incisor, only incompletely preserved in the holotype; it is posteriorly bordered by a relatively shallow and conical alveolus (the tooth being absent in all specimens at hand) separated from the medial one by bone and set at a relatively oblique angle (figs. 1C–D; 2C). Homologies of these teeth are uncertain, but the rodent-like medial tooth is surely an incisor, designated for description as  $i_1$ . The shape and disposition of the second alveolus agrees with the procumbent canine of Polydolopidae (Epidolopinae; cf. Paula Couto, 1952, 1961; Pascual & Bond, 1981) and Prepidolopidae (Pascual, 1980b, fig. 2D–E); it thus appears that this tooth is  $c_1$ . This alveolus is followed by a short diastema at alveolar level, then three cheekteeth, all rectangular in cross section (with some differences among them) and in close approximation, forming a molariform series. They are surrounded by enamel on all sides and are not strictly lobate, nor are the trigonid, talonid, or original cusps clearly indicated, as occlusion with the uppers was mediated through practically flat areas. The dentine forms a shallow basin surrounded by the highest enamel layer, which is slightly higher on the lingual side. There is a slightly deeper anteroposterior wear groove, extending from the anterolabial corner to the posterolingual one (fig. 1A). Grinding involved a longer propalinal movement and a shorter ectental stroke. The homologies of these teeth with the more numerous ancestral series cannot be determined. Plausibly

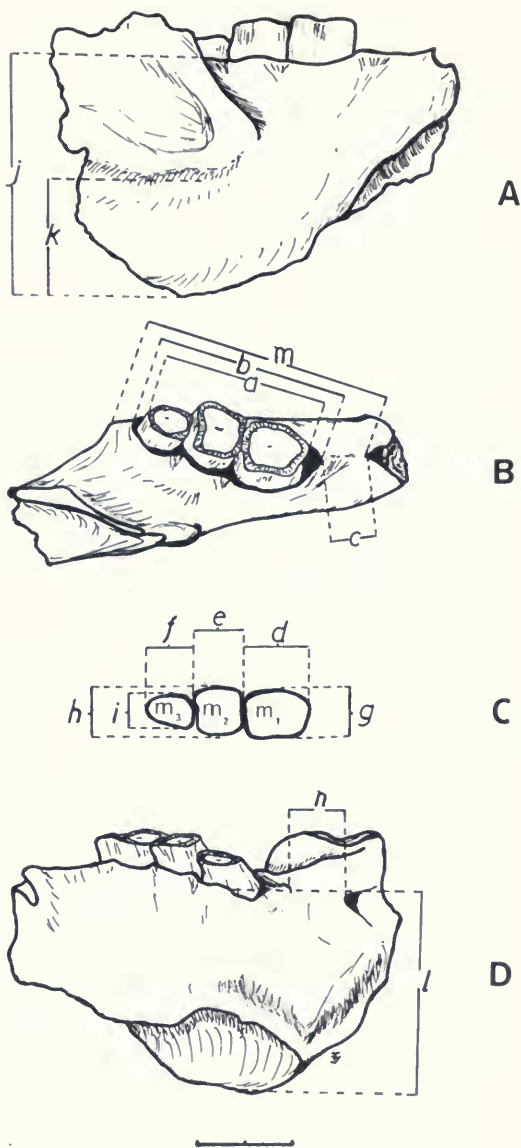


FIG. 3. *Patagonia peregrina* gen. et sp. nov. Outline of a right mandibular ramus fragment, with alveoli of  $i_1$  and  $c_1$ , and  $m_{1-3}$  complete (MACN CH-865), showing the measurements of Table 1. A, Labial view; B, occlusal view; C, cheekteeth series ( $m_{1-3}$ ); D, lingual view. Graphic scale = 2 mm.

they are homologous with those typically designated  $m_{1-3}$  in marsupials and are so designated here, yielding the lower dental formula 1.1.0.3, which is provisionally homologized as  $i_1, c_1, m_{1-3}$ . However, many specialized marsupials from the South American fossil record show tendencies (1)

TABLE 1. Dimensions of specimens of *Patagonia peregrina* gen. et sp. nov. (see fig. 3 for measurement references).

Specimen	Dimensions													
	a	b	c	d	e	f	g	h	i	j	k	l	m	n
MACN CH-864	...	...	...	...	1.00	...	1.00	0.96	...	...	...	...	...	...
MACN CH-865	3.68	4.08	1.40	1.40	1.20	1.08	1.08	1.12	0.96	5.40	2.80	...	6.20	1.80
MACN CH-866	...	...	...	...	1.00	1.08	...	1.00	0.92	...	...	...	...	1.60
MACN CH-867	...	...	1.12	1.20	1.00	...	0.96	0.96	...	...	...	...	...	...
MACN CH-868	...	4.08	...	...	1.00	1.00	1.04	1.00	0.92	...	...	...	...	1.80
MACN CH-869	3.60	...	...	1.36	1.08	1.00	0.96	0.96	0.92	5.12	3.00	4.60	...	...
MACN CH-870	...	...	...	1.40	1.00	...	1.00	1.00	...	...	...	...	...	...
MACN CH-874	...	...	...	...	1.08	...	...	0.96	...	4.80	2.20	4.40	...	...
MACN CH-875	...	...	...	...	1.28	1.16	...	1.24	1.08	6.76	...	...	...	2.40

to elongate or modify either the  $p_3$  (Polydolopidae and Parabderitini caenolestids; see Marshall, 1980) or the  $m_1$  (Abderitinae and Palaeothentinae caenolestids), and (2) to reduce (e.g., Caenolestidae) or lose (Polydolopidae) the  $m_4$ . All teeth except the  $c_1$  are completely hypselodont and rootless. The cheekteeth are slightly curved, with the concavity forward (fig. 1C–D).

**Incisor ( $i_1$ )**—Incompletely preserved in the holotype (fig. 2A–B). The anterior end is broken, but the posterior end is unaltered, showing an open pulp cavity with no sign of root formation. It is as elongate and curved as in the most specialized caviomorphs (e.g., Ctenomyidae), although not upcurved posteriorly. The extra-alveolar part would have been nearly vertical, although not so much as in the Groeberiidae (cf. fig. 4B,D). The tooth extends along the ventral border lingually, first beneath the  $m_1$  and then lingually to far below the  $m_3$ , terminating where the ventral border becomes an inflected flange (MACN CH-865, fig. 1B) reminiscent of kangaroos; the base of the alveolus shapes a superficial prominence similar to that of hystricognathous rodents, although enveloped by the inflected ventral border. It is approximately oval in cross section, with the long axis oriented dorsoventrally and with a flatter medial surface. Apparently enamel covers the entire tooth, but a noticeably heavier layer extends as a ventral band.

**Canine ( $c_1$ )**—None of the specimens in the hypodigm include this tooth, but its alveolus (figs. 1C–D; 2C) is oblique, tapered, and relatively shallow, indicating a closed-rooted tooth; its oblique orientation suggests that the occlusal apex was appressed against the occlusal tip of  $i_1$ .

**First Molar ( $m_1$ )**—The first molar is separated from the  $c_1$  by a crested diastema (fig. 1A) as long as  $m_1$ . It is the largest cheektooth, almost rectangular in cross section, with the longer lateral

faces slightly concave; the lingual face sometimes bears a very shallow groove along the intra-alveolar portion. The anterior face is convex, occasionally somewhat pointed; the posterior face is almost flat, forming angles with the lateral faces slightly greater than  $90^\circ$ .

**Second Molar ( $m_2$ )**—The second molar is irregularly quadrate, with the lateral faces slightly convex and the anterior and posterior ones flatter. The posterolingual angle is less than  $90^\circ$ , whereas the others are almost  $90^\circ$ . Its width is similar to that of  $m_1$  (fig. 1A).

**Third Molar ( $m_3$ )**—The third molar is the smallest cheektooth, being subtriangular in cross section rather than square. The anterior face is slightly convex, lingually flatter, and labially more strongly curved; the labial face converges posterolingually with the lingual face, forming a rounded pillar rather than a well-defined posterior face (fig. 1A).

**Mandible**—No nearly complete mandible is known, but parts of the horizontal ramus and base of the coronoid process are known. These parts indicate the mandible is extremely short and deep, like that of *Groeberia minoprioi*, although very different in other respects (cf. fig. 4B,D). The symphysis is subvertical and unfused, with a nearly smooth symphyseal surface (i.e., normal in structure instead of fused and forming the odd medial posterior projection peculiar to Groeberiidae). The depth of the mandible increases abruptly toward the  $m_3$ . The deep masseteric fossa appears to be peculiarly confined to a dorsal position, as the masseteric crest is situated at a level between the alveolar rim and the lowest level of the rounded and inflected ventral border (figs. 1B; 2A). A similar condition is found in some Abderitinae caenolestids (e.g., *Parabderites bicrispatus*; Marshall, 1976, fig. 8a), although in *P. bicrispatus* the mandibular body is not as deep and the alveolar border

not as extensively inflected. The coronoid process has its root beneath the  $m_2$ , forming a strong, salient lamina (known only by its root), so that a conspicuous diagonal valley is formed between the coronoid and the alveolar border behind  $m_3$  (fig. 1A); a similar structure is present in *Groeberia minoprioi* (see Patterson, 1952, p. 41); the valley is open labially and lingually limited by a prominence similar to that present in Australasian Potoroinae.

In many respects this strong, salient, ascending ramus and correlated features are reminiscent of highly fossorial caviomorphs, such as burrow-inhabiting Ctenomyidae. Although the mandibular angle is not preserved in any of the specimens, it probably was inflected, as suggested by the inflection of the ventral border, beginning at the level of  $m_3$ , which defines a lingual flanged crest (figs. 1B; 2B) similar to that producing the extremely inflected angle in the Macropodidae. This lingual ventral flanged crest seems to be the lingual border of an expanded and relatively deep pterygoid fossa, resembling that of argyrolagids (see Simpson, 1970a). There is a relatively large alveolar foramen within the pterygoid fossa, level with the alveolar border and within a pit (fig. 3D), and a mental foramen beneath the anterior face of  $m_1$  at the level of the alveolus of  $i_1$  (fig. 2A).

## Affinities

As in the case of *Groeberia* (see Simpson, 1970c), the conclusion that *Patagonia* is a marsupial rests on a combination of definite, negative, and indirect evidence. The most definite evidence for its being a marsupial is the inflected ventral border of the mandible and probably the related inflected angle. This evidence alone is inconclusive, as a few marsupials lack an inflected angle and a few placentals have one. However, no known placental has such an extended and upturned flange-shaped inflection, and even in marsupials it is rarely so well developed (e.g., Groeberiidae [Patterson, 1952], Argyrolagidae [Simpson, 1970a,b], and the Australasian Macropodidae). Unlike *Groeberia*, *Patagonia* has other characters supporting its marsupial affinities, namely the lower procumbent incisor-like canine. In the Epidolopinae (Pascual & Bond, 1981) there are three procumbent lower teeth, the third being unquestionably the canine. Within the more advanced Polydolopidae (Polydolopinae), there are one or three procumbent lower teeth; in the latter case, evidence suggests

they consist of two incisors and a canine, the medial incisor being quite reduced and the canine well developed, single, and closed-rooted.

As in *Groeberia* the negative evidence is that *Patagonia* has no features precluding its reference to the Marsupialia. It does exhibit characters making reference to any Eutheria highly improbable. Its habitus is rodent-like, but its two differentially procumbent lower teeth rule out reference to the Rodentia. While the incisor is rodent-like in shape, it is oriented differently than that in rodents, extending along the ventral border of the horizontal ramus, first below the  $m_1$ , then lingually to other molars, without curving upward. It apparently shapes the ventral border of the mandible. In addition, the short diastema extends at the level of alveoli. Among known rodents, only Paramyidae and Ischyromyidae developed diastemas at the alveolar level, but even in these groups, the incisor extends as in other rodents, not as in *Patagonia*. A more-or-less rodent-like habitus was also characteristic of some notoungulates, especially among Typotheria and Hegetotheria, but insofar as known not so extreme in development as in *Patagonia*. Neither the enlargement of the incisor nor the reduction of the cheekteeth is known in any primitive Paleocene notoungulates or in other South American "ungulates." Even later rodent-like notoungulates were much less specialized than the Oligocene *Patagonia*. South American marsupials diverged very early into unique evolutionary lineages (see Simpson, 1970a-c, 1971, 1980; Pascual, 1980a,b, 1981; Paula Couto, 1979; Reig, 1981).

*Patagonia peregrina* is unquestionably a marsupial because its unique and diagnostic combination of characters are unknown in any eutherian. Nevertheless, it could be regarded as another of the extinct South American mammals considered by some as *incertae sedis* and by others as a *tertium quid* with regard to the eutherian-marsupial dichotomy (McKenna, 1980; Reig, 1981). However, the marsupial affinities of other peculiar fossil mammals from South America remain unquestioned, despite weaker support than that offered here for *Patagonia*. For example, the basis for considering the Polydolopidae as marsupials is the combination of an inflected mandibular ramus, palatal vacuities, and a cheektooth formula of  $P \frac{1-3}{1-3}$  and  $M \frac{1-4}{1-4}$ . These characters were formerly used to exclude the polydolopids from the Allotheria. But, as these characters are present in primitive therians outside South America, their diagnosis of marsupials can be considered an "act of

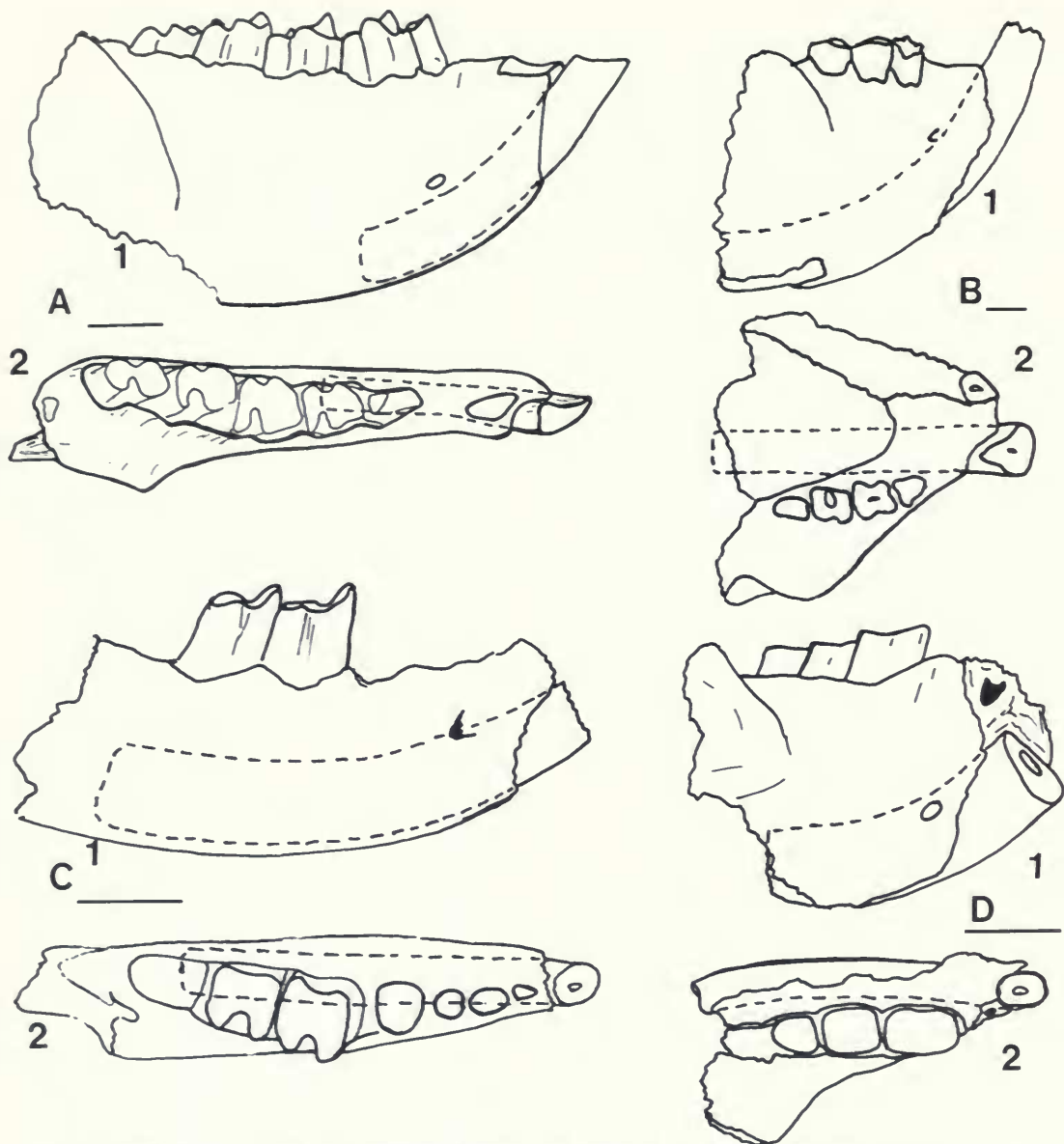


FIG. 4. Labial (1) and occlusal (2) outlines of mandibles, showing the different development of incisor. A, *Argyrolagus parodii* Rusconi; B, *Groeberia minoprioi* Patterson; C, *Proargyrolagus bolivianus* Wolff; D, *Patagonia peregrina* gen. et sp. nov. Graphic scale = 2 mm.

faith based on . . . geography and stratigraphic position rather than on . . . biology" (McKenna, 1980, pp. 58–59). We believe that assignment of polydolopids to marsupials represents the most parsimonious conclusion.

Like the newly described *Proargyrolagus bolivianus* (Wolff, 1984), *Patagonia peregrina* is another peculiar marsupial that appears in the fos-

sil record without known ancestors (see Simpson, 1970c, p. 16) only to vanish again soon afterward: Groeberiidae (Divisaderan Age, Late Eocene); Patagoniidae (Colhuehuapian Age, Late Oligocene); Necrolestidae (Santacrucian Age, Early Miocene); Argyrolagidae (Huayquerian to Uquian Ages, Late Miocene to Early Pleistocene). We believe there are cogent reasons to think of *Proargyrolagus bo-*



*livianus* Wolff, 1984, described as a Deseadan argyrolagid, as possibly representing a distinct family of Argyrolagoidea.

This raises the question of the position of *Patagonia* among the varied ranks of South American marsupials. The previous descriptions and illustrations demonstrate that *Patagonia peregrina* has many peculiarities that are rare, differently developed, or completely absent in other marsupials (cf. fig. 4). The most striking of these are:

1. Mandible extremely short and deep, with unfused subvertical symphysis, dorsally positioned masseteric fossa, ventral border inflected at level of the  $m_3$ , enveloping there the alveolus of the incisor.
2. Presence in each ramus of mandible of one rodent-like rootless incisor that extends lingually along ventral border of mandible to below the  $m_3$ .
3. Presence in each ramus of one procumbent canine, single- and closed-rooted, scarcely separated from the incisor and with the occlusal apex probably appressed to the incisive apex.
4. Three rectangular and continuously growing cheekteeth arranged in close sequence.

These and other less striking characters underscore the unique specializations of *Patagonia peregrina*, leading to its assignment to a new family, Patagoniidae. But the distinctive combination of characters in the Patagoniidae identify it as a distinct evolutionary group, that is, a different cladogenetic unit. Simpson (1945, 1970a, 1980) designated natural evolutionary groups of marsupials as superfamilies. Following this line of reasoning, Patagoniidae should be allocated to a new superfamily, the Patagonioidea.

What are the affinities of this new superfamily to other superfamilies within the superorder Marsupialia? Any discussion of its affinities depends on the systematics of other taxa, many of which are problematic. The systematics of fossil and extant South American marsupials, including the merits of recognizing Marsupialia as a superorder, are discussed by Simpson (1970a, 1971) and Pascual (1980b).

The majority of South American marsupials represent the order Polyprotodonta; this is roughly equivalent to Ride's (1964) Marsupicarnivora, but also includes Ameghino's Paucituberculata (see Pascual, 1980b; *contra* Kirsch, 1977a,b; Reig, 1981). There is as yet no compelling argument to

include any South American families within the Australasian order Diprotodonta (Reig, 1981), despite some suggestions to the contrary (e.g., Pascual & Herrera, 1973, 1975). While the allocations of these groups seems unambiguous, the positions of most remaining groups (e.g., Argyrolagidae, Necrolestidae, and Groeberiidae) remain uncertain. With some reservation, Kirsch (1977b) included the Necrolestidae in the polyprotodont Borhyaenoidea (as did Patterson, 1958), and the Groeberioidea and Argyrolagoidea within the Paucituberculata. Independently, Clemens and Marshall (1976) also treated these animals as marsupials, recognizing each as superfamilies: Argyrolagoidea, Necrolestoidea, and Groeberioidea. Like Simpson, they made these assignments with disclaimers that the interrelationships of these groups were far from clear.

Reig (1981, p. 60) not only questioned whether the Argyrolagidae (his Microtragulidae) were marsupials, as none of its known characters are typologically diagnostic, but conjectured probable affinities to the Anagalida. Further, without rigorous analysis, he suggested that the Argyrolagidae could be treated as an independent order, proposing the name Argyrolagida. He concluded that only more intensive study or additional records could substantiate allocation of this order to the Metatheria or the Eutheria.

Remains of Patagoniidae exhibit a unique mosaic of characters, some of which are absent or differently developed in Groeberiidae and Argyrolagidae. Despite their similarities, each of these taxa appears *prima facie* to represent independent evolutionary trends. To assess their interrelationships, common and distinctive characters of each must be carefully weighed. Remains of Argyrolagoidea obtained in the same horizon and locality as the hypodigm of *Patagonia peregrina* should be particularly useful in this regard and are now under study. Ordinal and subordinal allocation of the Patagonioidea await this more comprehensive analysis. Known representatives of this taxon are so highly derived, as is the case with other peculiar marsupials, that their relationships to other marsupial groups are obscure and can only be clarified by an expanded record of earlier forms.

## Ecology and Historical Biogeography

Biological inferences of *Patagonia* are necessarily limited to the mandibular fragments thus far

known. These demonstrate unique characters among marsupials, living or extinct, which are obviously related to a particular mode of life. No known eutherian possesses such mandibular features. Superficially it is similar to *Groeberia*, both being rodent-like marsupials: each has a short and deep mandible with a single enlarged, open-rooted incisor, deeply extended along the mandible, with the extra-alveolar part apparently nearly vertical. These represent functional not phylogenetic similarities, as similar states were attained by different routes: in *Groeberia* this tooth extended within an odd medial posterior projection of the symphysis, whereas in *Patagonia* the intra-alveolar portion is truly rodent-like, in being extended along the horizontal ramus (cf. fig. 4B,D). No doubt both were powerful gnawers as the lower incisor worked almost vertically, much more so than in most rodents. The unknown face and snout of *Patagonia* was probably short and deep; whether it had two pairs of lagomorph-like upper incisors like *Groeberia* remains unknown. Related to this gnawing specialization, both *Groeberia* and *Patagonia* show a short diastema near the alveolar level and a reduced number of postincisive teeth, four in both; however, *Patagonia* has three cheekteeth, whereas *Groeberia* has four. The rodent-like habitus of *Patagonia* is especially advanced, because the three cheekteeth are truly hypselodont, rectangular-shaped in cross section, with at most only shallow lateral grooves representing the remnants of ancestral bilobate cheekteeth.

This combination of features suggests food was obtained by gnawing and prepared for swallowing by grinding. It represents extraordinary convergence on some desert-adapted and fossorial forms, such as the Octodontidae. The evolution of cheekteeth toward a rectangular shape and numerically reduced sequence has been recognized as occurring within the Octodontoidea (from the Octodontidae to the Ctenomyidae; Pascual et al., 1965). The dental features of *Patagonia* are also convergent on those of the desert-dwelling African Bathyerigidae, particularly to the sand rat *Heterocephalus glaber*, and to the North American Geomyidae. These convergent anatomical features suggest that Patagoniidae were probably fossorial marsupials.

Anatomical convergence of *Patagonia* on desert-dwelling fossorial rodents is curious, because prevailing conditions in central Patagonia during the Colhuehuapian Age were not highly favorable to desert dwellers. The first record of platyrrhine monkeys in Patagonia occurs at the same locality and level (Fleagle & Bown, 1983) as *Patagonia*.

Many other vertebrate remains recovered at this site (see Bordas, 1939; Donadío, 1983) suggest an environment of well-watered tropical woodlands. Conversely, however, both Argyrolagoidea and very advanced Cephalomyidae rodents from this site (currently under study) show dental features reminiscent of desert or at least drier environments. Generally, the Colhuehuapian vertebrate fauna from central Patagonia (see Pascual, 1970; Pascual & Odreman Rivas, 1971; Marshall et al., 1983) is composed of both forest and open-country types, presumably brought together in a subtropical savanna. Thus, the Patagoniidae, Cephalomyidae, and Argyrolagoidea occurred in apparently inappropriate environments, probably restricted to xeric patches in the subtropical savanna mosaic. Because the Colhuehuapian Patagoniidae were already highly specialized for xeric habitats, they probably evolved earlier in the Paleogene. It therefore seems likely that ancestral forms existed in the Deseadan (Early Oligocene). Another highly specialized group of marsupials, the Argyrolagoidea, suggests this hypothesis. Formerly believed present in the record from the Huayquerian (Late Miocene) to the Uquian (Early Pleistocene; see Marshall et al., 1983), argyrolagooids have now been reported from the Deseadan of Bolivia (Wolff, 1984), and here from the Colhuehuapian beds of central Patagonia.

The pre-Deseadan record contains no potential ancestor for either Argyrolagoidea or Patagoniidae. Simpson (1970c, p. 17) proposed that "these groups (including Groeberioidea) evolved in what are now (and quite likely were then) the tropics and are picked up in our record only when they spread rather briefly to what was for them a marginal area." It seems quite probable that the environments responsible for their initial divergence were poorly or not represented in the known fossil record.

Global diastrophic movements in the Late Eocene, and apparently related climatic and environmental changes, are thought to be responsible for the cosmopolitan turnover in Early Oligocene mammal communities (Kurtén, 1971). This turnover also occurred in South America (Pascual, 1984). Mammal communities in the Deseadan (Early Oligocene) are substantially different from Eocene communities in composition (see Pascual et al., 1985), apparently reflecting Stehlin's "*grande coupure*." The apparently sudden occurrence of the Argyrolagoidea, and probably the Patagoniidae, in the Deseadan Age is probably another example of this global turnover.

It is remarkable that, to the numerous successive parallel trends ("successive trends" or "iteration"; Simpson, 1953, pp. 248–259; 1961, p. 127) in the evolutionary history of South American mammals, especially from the Deseadan on, can be added the convergence of Oligocene patagoniid marsupials and Pliocene to Recent ctenomyid rodents on a common morphology. These convergences are products of similar responses to repeated environmental conditions. The anatomical and functional similarities of *Patagonia peregrina* with the extant *Ctenomys* are so striking that we are tempted to call the former the "marsupial tucucu."

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